

# CONTRIBUTIONS TO THE GENUS *FESTUCA* (POACEAE: POEAE) IN MEXICO AND A KEY TO THE CENTRAL AMERICAN SPECIES

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## ABSTRACT

A new species, ***Festuca longiligula*** (Poaceae: Poeae), is described from the state of Coahuila, Mexico. Names and descriptions are provided for two nothospecies from central Mexico, ***Festuca xgonzalez-ledesmae*** and ***F. xmiscella***, putative hybrids of *F. livida* × *F. hephaestophila* and *F. livida* × *F. tolucensis*, respectively. Observations on some unusual morphological characteristics of *Festuca* (subgenus *Helleria*) *livida* are presented. A key to the known species of *Festuca* in Central America is provided.

KEY WORDS: *Festuca*, new species, Mexico, Central America, hybridization, nothospecies, subgenus *Helleria*, keys

## RESUMEN

Se describe una nueva especie, ***Festuca longiligula*** (Poaceae: Poeae), del estado de Coahuila, México. Se dan nombres y descripciones de dos nothospecies de México central, ***Festuca xgonzalez-ledesmae*** y ***F. xmiscella***, híbridos putativos de *F. livida* × *F. hephaestophila* y *F. livida* × *F. tolucensis*, respectivamente. Se presentan observaciones de algunas características morfológicas inusuales de *Festuca* (subgénero *Helleria*) *livida*. Se aporta una clave de las especies conocidas de *Festuca* en América Central.

The pioneering work of E.B. Alexeev on the taxonomy of *Festuca* in Mexico and Central America (Alexeev 1980, 1984) set the ground work for further detailed investigations on the genus. Not all of his described taxa have been widely accepted (cf. Soreng et al. 2003) and some await further study. A working list of species is given in Table 1. This paper describes new species (including nothospecies), contributes some additional observations and presents an updated key to the species known from Mexico and Central America.

***Festuca longiligula*** S.J. Darbyshire, sp. nov. (**Figs. 1, 2A, 2B, 3A**) TYPE: MEXICO. COAHUILA: SO de Saltillo, ceja y ladera S de Sierra La Viga, subalpina, 3700 msnm, 22 Aug 1986, [A.] McDonald 2102 (HOLOTYPE: TEX: ISOTYPE: WIS, XAL (non vidi).

Plantae perennes caespitosae, innovationibus intravaginalibus praeditae. Culmi 70–90 cm alti, leves. Vaginae foliorum ima basi tantum integrae, leves vel scabrae; vaginae foliorum emortuorum in fibras longitudinales non solutae; ligulae scariosae, (2–)5–9.5 mm longae, laceratae; laminae foliorum innovationum conduplicatae, 0.8–1.5 mm diametri, abaxialiter scabrae, adaxialiter hirsutae, cum 9–11 nervis, 7–11-costatae, sclerenchymate abaxialiter annulo continuo subepidermali disposito, sclerenchyma fasciculis cum venas majore abaxialiter et interdum adaxialiter conjunctis, cellulis bulliformibus destitutae vel cellulae minutae. Paniculae 10–22 cm longae, pyramidales, laxae, axe distali et ramulis scabris. Spiculae (6–)7.5–13 mm longae, ovatae ad ellipsiodeae, cum 4–7 flosculis; glumae ovatae ad lanceolatae, scariosae vel margine late scariosae, glabrae vel pleurumque scabrosae ad hispidulae dimidio superanti; glumae inferiores 3.4–5.5(–5.7) mm longae, cum 1(3) nervis; glumae superiores 4.5–6.5 mm longae, cum (1–)3(–5) nervis; rachillae usque ad 1.5 mm longae, hispidulae unilateraliter; lemmatae (5–)6–7 mm longae, lanceolatae ad anguste ovatae, glabrae vel apice scabra ad hispidula, cum 5(–7) nervis obscuris, apice late scariosa, obtusa ad abrupte acuta, interdum emarginata ad plus minusve bidentata, inermia vel praedita interdum arista brevissima usque ad 0.5 mm longa; paleae 5–7 mm longae, apice bidentatae, inter venas et saepe in marginalibus distalibus hispidulae, venae scabroso-ciliatae prope apicem ad 1/2; antherae 2.5–3.3 mm longae; ovarium apex sparsim hispidulus. Caryopses 3.5–4.5 × 0.8–1.5 mm.

**Plants** perennial, caespitose, shoots intravaginal. **Culms** erect or slightly decumbent at the base, 70–90 cm tall, smooth and glabrous. **Leaf sheaths** with the margins closed only at the base, smooth and glabrous or sometimes scabrous, not decaying into longitudinal fibres; **auricles** absent; **ligules** scarious, (2–)5–9.5 mm long, lacerate; **leaf blades** of vegetative shoots conduplicate, 0.8–1.5 mm in diameter, abaxially scabrous, adaxially hirsute, with 9–11 veins and 7–11 adaxial ribs; **sclerenchyma** in a continuous abaxial band, fascicles joining the major veins with abaxial epidermis and with adaxial fascicles opposite veins sometimes joining veins to form girders (Fig. 2); bulliform cells absent or inconspicuous. **Inflorescence** paniculate,

TABLE 1. Species of the genus *Festuca* in Mexico and Central America and known distributions (primarily from literature sources).

Species	Mexico (States)	Central America (other countries)
<b><i>F. aequipaleata</i></b> E. Fourn., Biol. Centr.-Amer. 3(20):581. 1885.	Veracruz	
<b><i>F. aguana</i></b> E.B. Alexeev, Bot. Zhurn. (Moscow & Leningrad) 66:1493, f. 1. 1981.	?	Guatemala, Panama
<b><i>F. amplissima</i></b> Rupr., Bull. Acad. Roy. Sci. Bruxelles 9:236. 1842.	Chiapas, Distrito Federal, Durango, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Nuevo León, Puebla, Tlaxcala, Veracruz	Costa Rica, Guatemala, Panama
<b><i>F. arundinacea</i></b> Schreb., Spicil. Fl. Lips.:57. 1771.	México, Veracruz	Costa Rica, Guatemala
<b><i>F. asperella</i></b> E.B. Alexeev, Bot. Zhurn. (Moscow & Leningrad) 66:1496–1497, f. 1. 1981.	México	
<b><i>F. bajacaliforniana</i></b> Gonz.-Led. & S.D. Koch, Novon 4:28–30, f. 3. 1994.	Baja California	
<b><i>F. beamanii</i></b> E.B. Alexeev, Bot. Zhurn. (Moscow & Leningrad) 66:1500–1501, f. 2. 1981.		Guatemala
<b><i>F. bidenticulata</i></b> E.B. Alexeev, Bot. Zhurn. (Moscow & Leningrad) 66:1496, f. 1.1981.	Veracruz	
<b><i>F. breviglumis</i></b> Swallen, Contr. U.S. Natl. Herb. 29:398. 1950.	Jalisco, Michoacán, Morelos, Oaxaca	Costa Rica, Guatemala, Panama
<b><i>F. callosa</i></b> (Piper) St. Yves, Candollea 2:291. 1925.	Oaxaca, Puebla	
<b><i>F. cartagana</i></b> E.B. Alexeev, Bot. Zhurn. (Moscow & Leningrad) 67:1291–1292, f. 1. 1982.		Costa Rica, Panama
<b><i>F. chiriquensis</i></b> Swallen, Ann. Missouri Bot. Gard. 30:116. 1943.		Costa Rica, Panama
<b><i>F. coahuilana</i></b> Gonz.-Led. & S.D. Koch, Novon 4: 27–27, f. 2. 1994.	Coahuila	
<b><i>F. diclina</i></b> Darbysh., Novon 5:129, f. 1, 2. 1995.	Chihuahua	
<b><i>F. filiformis</i></b> Pourret, Hist. & Mém. Acad. Roy. Sci. Toulouse 3:319. 1788.		Costa Rica
<b><i>F. xgonzalez-ledesmae</i></b> Darbysh.	México, Tlaxcala, Veracruz	
<b><i>F. guatemalica</i></b> E.B. Alexeev, Bot. Zhurn. (Moscow & Leningrad) 66:1498–1500, f. 2. 1981. [= <i>F. willdenowiana</i> ?]	México	Guatemala
<b><i>F. hephaestophila</i></b> Steud., Syn. Pl. Glumac. 1:310. 1854.	México, Nuevo León, Puebla, Tamaulipas, Tlaxcala, Veracruz	Costa Rica, Guatemala
<b><i>F. herrerae</i></b> Davidse, Novon 2:322–324, f. 1. 1992.		Costa Rica, Panama
<b><i>F. hintoniana</i></b> E.B. Alexeev, Bot. Zhurn. (Moscow & Leningrad) 67:1292, f. 1. 1982.	Coahuila, Nuevo León	
<b><i>F. jaliscana</i></b> E.B. Alexeev, Bot. Zhurn. (Moscow & Leningrad) 66:1493–1495, f. 1. 1981.	Jalisco	
<b><i>F. ligulata</i></b> Swallen, Amer. J. Bot. 19:436, f. 1. 1932.	Coahuila	
<b><i>F. livida</i></b> (Kunth) Spreng., Syst. Veg. 1:353. 1825.	México, Puebla, Tlaxcala, Veracruz	
<b><i>F. longiligula</i></b> Darbysh.	Coahuila	
<b><i>F. lugens</i></b> (E. Fourn.) Hern.-Xol., Bol. Soc. Bot. Mexico 23:165. 1958.	Chiapas, Chihuahua, Distrito Federal, Hidalgo, Jalisco, México, Michoacán, Morelos, Oaxaca, Puebla, San Luis Potosí, Tamaulipas, Veracruz	Honduras
<b><i>F. xmiscella</i></b> Darbysh.	México	
<b><i>F. orizabensis</i></b> E.B. Alexeev, Bot. Zhur. 66: 1497–1498, f. 2. 1981.	Distrito Federal, Durango, Jalisco, México, Puebla, Veracruz	
<b><i>F. ovina</i></b> L., Sp. Pl. 1:73–74. 1753.		Costa Rica
<b><i>F. panamica</i></b> E.B. Alexeev, Bot. Zhurn. (Moscow & Leningrad) 67:1290–1291, f. 1. 1982.		Panama

TABLE 1. continued.

Species	Mexico (States)	Central America (other countries)
<b>F. pringlei</b> St. Yves, Candollea 2:305–307, f. 53. 1925.	Chihuahua, Durango, Jalisco, San Luis Potosí	
<b>F. roblensis</b> Gonz.-Led., Novon 8:147–149, f. 1. 1998.	Guanajuato, Zacatecas	
<b>F. rosei</b> Piper, Contr. U.S. Natl. Herb. 10:45. 1906.	Distrito Federal, Guerrero, Jalisco, México, Michoacán, Morelos, Tlaxcala, Veracruz	Guatemala
<b>F. rubra</b> L., Sp. Pl. 1:74. 1753.	Chihuahua, México, Nuevo León	Costa Rica
<b>F. rzedowskiana</b> E.B. Alexeev, Bot. Zhurn. (Moscow & Leningrad) 66:1500, f. 2. 1981.	México	
<b>F. subverticillata</b> (Pers.) E.B. Alexeev, Novosti Sist. Vyssh. Rast. 17:52, f. 2. 1980.	based on a probable label error	
<b>F. wallenii</b> E.B. Alexeev, Bot. Zhurn. (Moscow & Leningrad) 66:1495–1496, f. 1. 1981.		Panama
<b>F. talamancensis</b> Davidse, Novon 2:324, f. 1. 1992.		Costa Rica
<b>F. tancitaroensis</b> Gonz.-Led. & S.D. Koch, Novon 4:25–27, f. 1. 1994.	Michoacán	
<b>F. tolucensis</b> Kunth, Nov. Gen. Sp. 1:153. 1815.	Chiapas, Distrito Federal, Jalisco, México, Michoacán, Morelos, Oaxaca, Puebla, San Luis Potosí, Tlaxcala, Veracruz	Costa Rica, Guatemala
<b>F. valdesii</b> Gonz.-Led. & S.D. Koch, Novon 8: 149–151, f. 2. 1998.	Coahuila, Nuevo León, Tamaulipas	
<b>F. willdenowiana</b> Schult. & Schult. f., Add. ad Mant. 3:650. 1827.	Distrito Federal, México, Michoacán, Puebla, Tlaxcala, Veracruz	Guatemala

10–22 cm long, pyramidal, lax, rachis glabrous below and scabrous above; branches lax, 1(–2) per lower node, scabrous. **Spikelets** (6–)7.5–13 mm long, ovate to ellipsoid, more or less distal on the branches, with 4–7 florets; **glumes** ovate to lanceolate, scarious or with broad scarious margins, glabrous or frequently scabrous to hispidulous in the upper half; **lower glumes** 3.4–5.5(–5.7) mm long, with 1(–3) veins; **upper glumes** 4.5–6.5 mm long, with (1–)3(–5) veins; **rachilla** up to 1.5 mm long, unilaterally hispidulous opposite to the floret; **lemmas** (5–)6–7 mm long, lanceolate to narrowly ovate, glabrous or apically scabrous or hispidulous, with 5(–7) obscure veins, the apex broadly scarious, obtuse to abruptly acute, sometimes emarginate to more or less bidentate, awnless or with a short mucro arising between the lobes to 0.5 mm long; **paleas** 5–7 mm long, bidentate, apically hispidulous between the veins and sometimes on the upper margins, veins scabrous-ciliate in the upper 1/2–2/3; **anthers** 2.5–3.3 mm long; **ovary** apex sparsely hispidulous; styles 2. **Caryopses** 3.5–4.5 mm long, 0.8–1.5 mm wide.

Additional collection examined: **MEXICO. Coahuila:** Mpio. de Arteaga, Sierra la Viga 6 km al E de Jame, Puerto Maravillas, 25°22'N 100°34'W, bosque de *Pinus rudis*, *P. ayacahuite*, *Pseudotsuga*, *Abies*, *Quercus*, con arbustos de *Ceanothus* y *Pinus culminicola*, 3000–3150 m, 16 Sep 1989, J.A. Villarreal & et al. VR-1983 (TEX). Fig. 2B.

*Festuca longiligulata* belongs to subgenus *Festuca* section *Breviaristatae* and is similar to *F. thurberi* Vasey of the southern Rocky Mountains in the dense caespitose habit, glumes thinner in texture than the lemmas and long ligules. It differs from the latter in the more ovate lemmas which are obtuse (sometimes abruptly acute) to somewhat truncate or emarginate with a wide scarious margin, while in *F. thurberi* the lemmas are more narrowly ovate to lanceolate and tapering to an entire acute apex with narrow scarious margins (Fig. 3). The anthers of *F. longiligulata* are usually shorter, 2.5–3.3 mm, versus 3–4.5 mm, and the ovary apex is sparsely hispidulous, versus densely hispidulous. These characters and the isolated distribution in the Sierra Madre Oriental suggest that *F. longiligula* is a distinct species. It differs from *F. ligulata* in the more densely caespitose habit, usually longer ligules ((2–)5–9.5 mm, versus 2.5–3.5 mm), lemmas (5–7 mm, versus 4.5–6 mm) and anthers (2.5–3.3 mm, versus 1.5–2.6 mm).



FIG. 1. *Festuca longiligula* holotype specimen, McDonald 2102 (TEX). Scale bar: left = 2 inches; right = 5 cm.

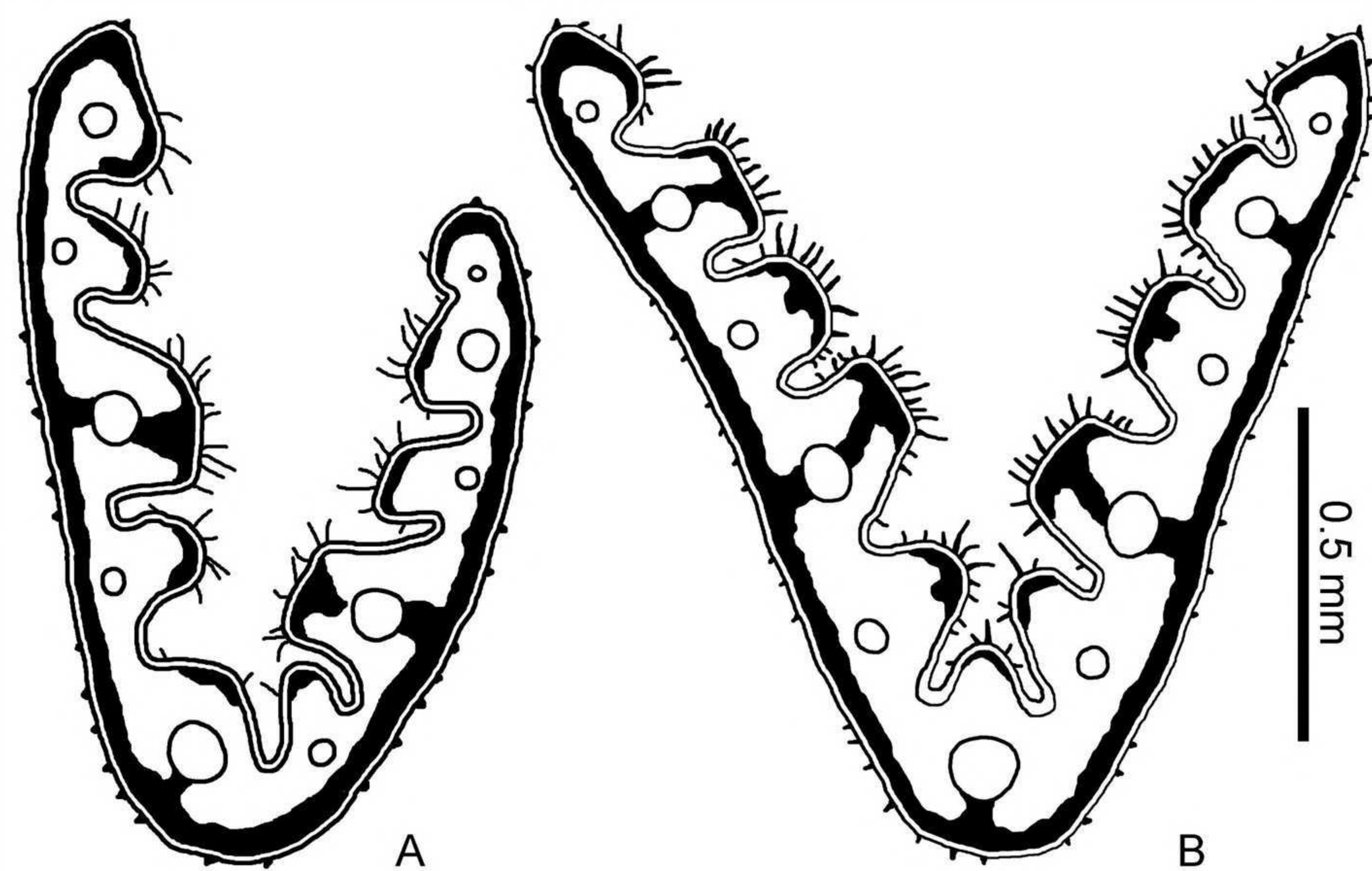


FIG. 2. Innovation shoot leaf blade cross sections of *Festuca longiligula*. A – Holotype, McDonald 2102; B – Paratype, Villarreal et al. VR-1983.



FIG. 3. Lower lemmas. A – *Festuca longiligula*, McDonald 2102 (holotype); B – *Festuca thurberi*, Swallen 6608 (DAO).

***Festuca* subgenus *Helleria***

In his surveys of *Festuca* Alexeev (1980) established *F.* subgenus *Helleria* (E. Fourn.) E.B. Alexeev (Novost. Sist. Vyssh. Rast. 17:51. 1980;  $\equiv$  *Helleria* E. Fourn., Mex. Pl. 2:128. 1886, non Nees & Martius, 1824; *Hellerochloa* Rauschert, Taxon 31:561. 1982) in which he included *F. livida* as the sole species. The long glumes (longer than the lemmas and usually enclosing the whole spikelet) and the unusual strongly drooping panicles were cited as uniquely distinctive characteristics within the genus *Festuca*. Alexeev interpreted these characteristics as a highly specialized cryomorphic adaptation to the alpine habitats in which the species occurs. Other characteristics of *F. livida* are similarly advantageous in these rigorous climatic conditions. The small anthers (0.8–1.5 mm long) and usually non-exserted stamens and stigmas are typical of a cleistogamous habit. The anthers dehisce at an early stage of inflorescence development with pollen being released into the cavity

between the lemma and palea. The anthers dehisce at the level of the stigmas and remain entangled in the stigmatic branches as the caryopsis matures. The leaf sheaths of shoots and culms are loose (inflated), trapping air and providing insulation for the developing tissues within. Other Central American alpine species of *Festuca* have loose flag leaf sheaths, but this characteristic is pronounced in *F. livida*.

The pendulous form of the panicle in *F. livida* is unusual in that the rachis is lax right to the lowest inflorescence node. The lowest rachis internode is scarcely wider than the single branch at the lower node, giving the inflorescence the appearance of consisting of two branches at the lower node. As in many species of *Festuca* there is a ring of tissue associated with the lowest inflorescence node. In *F. livida* it is usually well developed bearing a pointed tip and sometimes extending into short bract up to 25 mm long. In other Central America species of *Festuca*, the ring of tissue may bear a pointed tip, but it is scarcely more than 1 mm long. Another unusual characteristic of *F. livida* is the distinctly swollen and slightly flattened upper culm internode with a large inner cavity (Fig. 4).

Two chromosome counts have been reported for *F. livida*,  $n = 14$  (Nevado de Toluca; Beaman et al. 1962) and  $n = 21$  (Cofre de Perote; González-Ledesma 1991). Meiosis of plants from Cofre de Perote was, however, disrupted (González-Ledesma 1991), indicating pollen fertility problems. Pollen from anthers of 9 herbarium specimens (DAO) showed a considerable range of development and stainability in lactophenol cotton blue preparations. Even though most anthers seemed to be normally dehiscent, conservative estimates of pollen viability ranged from 0–20%. When slightly less stained and/or non-spherical (but not collapsed) grains were deemed to be possibly fertile, calculations suggested that 2–48% of pollen grains might be viable. However, low pollen viability does not necessarily present a fertility handicap for cleistogamous grasses and may in fact be an adaptive conservation of resources. Field observations in 1997 at Cofre de Perote (19°29'42"N, 97°08'55"W) and La Malinche indicated that large numbers of plants bore inflorescences with abortive caryopses, although most florets usually contained dehiscent anthers. It is possible that unusual climatic conditions in that season caused caryopsis abortion, although given the low proportion of stainable pollen, lack of caryopsis development may have been the result of failed pollination.

The many specialized morphological and anatomical features of *F. livida*, unique or highly unusual in *Festuca*, provide support for the recognition of the separate genus *Hellerochloa*. However the taxon is clearly related to the members of *Festuca* subgenus *Festuca*, as indicated by the similarity of the vegetative shoot structure, leaf blade anatomy (both in cross section and the abaxial epidermis) and ovary/caryopsis morphology, as well as the spontaneous hybridization with at least *F. hephaestophila* and *F. tolucensis* (see below). In spite of the fact that intergeneric hybrids have been reported between most genera in Loliinae (except *Leucopoa*) and many genera in Poeae, and that *F. livida* exhibits several unique or unusual characters, the recognition of *Hellerochloa* seems premature.

Two spontaneous hybrids, *F. livida* × *F. hephaestophila* and *F. livida* × *F. tolucensis* are sterile, intermediate in many morphological characters and not uncommon in areas where the parental species come into contact. How the largely cleistogamous *F. livida* is able to hybridize with sympatric species of *Festuca* is yet to be determined.

***Festuca xgonzalez-ledesmae*** S.J. Darbyshire, nothosp. nov. (*Festuca livida* (Kunth) Willd. ex Spreng. × *Festuca hephaestophila* Nees ex Steudel). (**Fig. 5**). TYPE: MEXICO. VERACRUZ: Mpio. de Perote, Cofre de Perote, lado N en la base del macizo rocoso que esta en la cima, pastizal de *Festuca*, *Calamagrostis*, *Trisetum*, *Agrostis* y *Deschampsia*, alt. 4050 m, 15 Sep 1986, M. González-Ledesma & P. Vera C. 196 (HOLOTYPE: DAO 683891; ISOTYPE: CHAPA).

Inter *Festuca livida* et *Festuca hephaestophila* intermedia est. Plantae perennes caespitosae, interdum rhizomatibus brevibus praeditae, innovationibus intravaginalibus praeditae. Culmi 4.5–22 cm alti, erecti, glabri, internodia superne interdum leviter tumida. Vaginae foliorum ima basi tantum integrae, leves, plus minusve inflatae; vaginae foliorum emortuorum in fibras longitudinales plus minusve solutae; ligulae 0.2–1(–1.5) mm longae; laminae foliorum conduplicatae, (0.3–)0.4–0.9 mm diametri, apice acuto ad obtuso, abaxialiter glabrae, adaxialiter hirsutae, cum 5–7 nervis, 5–7-costatae, sclerenchyma fasciculis marginalibus, cum venas majore abaxialiter, raro adaxialiter conjunctis, cellulis bulliformibus destitutae. Paniculae (2–)3–6 cm longae, plus minusve erectae, axe distali et ramulis scabris. Spiculae 7–11(–13) mm longae, ellipsoideae, cum (2–)3–4(–5) flosculis; glumae glabrae ad scabrae vel hispidulae, subulatae ad lanceolatae vel tantum ellipsoideae, inermes vel arista usque ad 0.3 mm longa praeditae; glumae inferiores (5.8–)6.5–8.5(–9) mm longae, lanceolatae vel ovatae, cum 1–3 nervis; glumae superiores (6.5)7–9.5(–10) mm longae, cum 3–5 nervis; rachillae usque ad 1.5

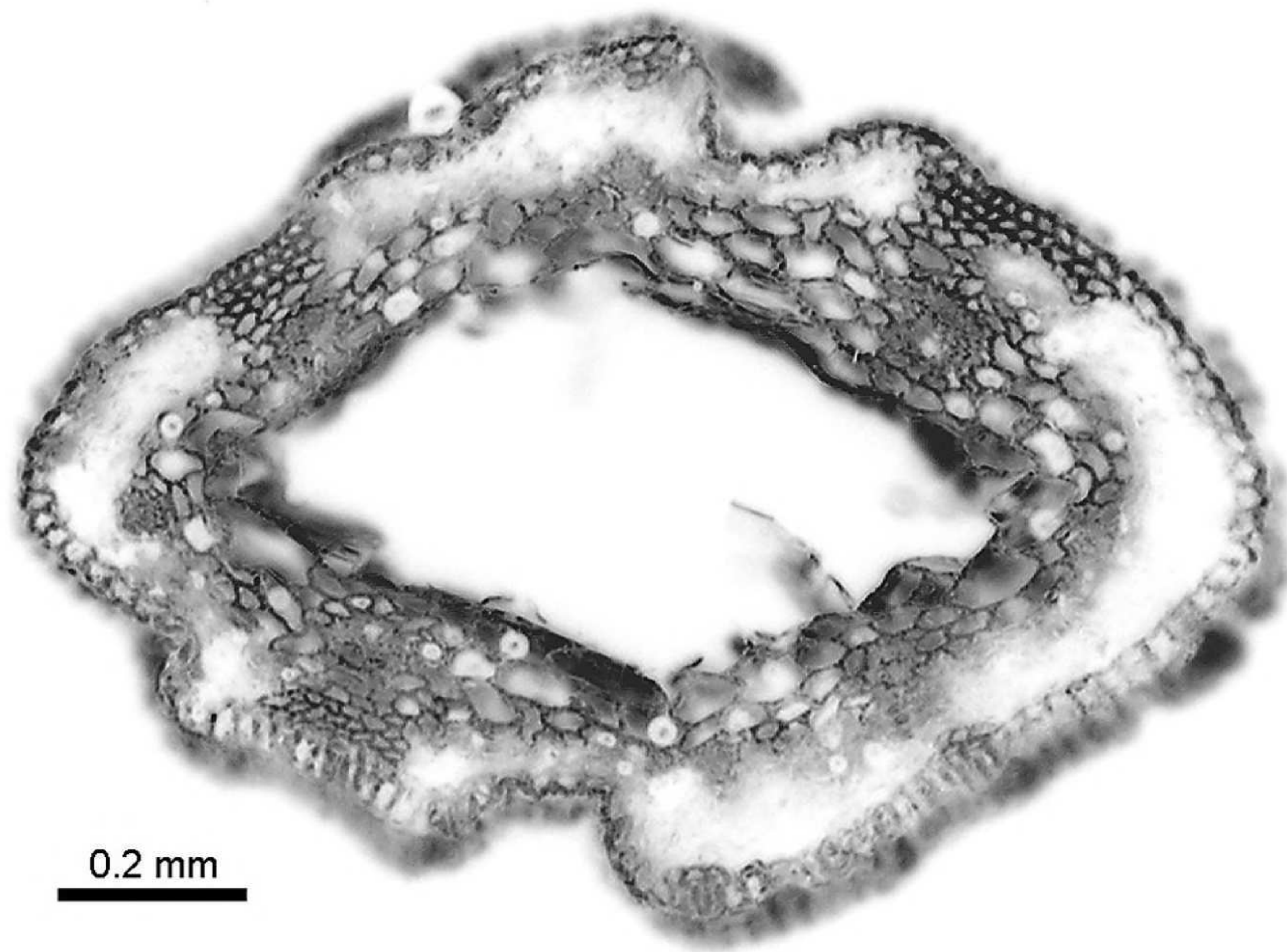


FIG. 4. *Festuca livida*, hand cross section of upper culm internode about 1 cm from apex.

mm longae, hispidulae unilateraliter; lemmatae 6.5–8.5(–9.5) mm longae, lanceolatae ad ellipsoideae, scabrae ad hirsutae, cum 5 nervis, apice interdum bidentata, inermia vel plerumque praedita arista (0.3–)0.8–2.5(–3.4) mm longa; paleae 5.5–7.5 mm longae, inter venas et saepe in marginalibus distalibus hispidulae, venae prope apicem ad 2/3(–3/4) cum trichomatibus; antherae (1–)1.2–2 mm longae, plerumque indehiscentes; ovarium apex glabrus vel sparsim hispidulus. Caryopses non praeditae.

Intermediate between *F. livida* and *F. hephaestophila*. **Plants** perennial, densely caespitose, short rhizomes sometimes present, shoots intravaginal. **Culms** 4.5–22 cm tall, erect, glabrous throughout, upper internode sometimes slightly swollen. **Leaf sheaths** closed only at the base, glabrous, more or less loose and disintegrating into fibres with age; **ligules** 0.2–1(–1.5) mm long; **leaf blades** conduplicate, (0.3–)0.4–0.9 mm in diameter, apex abruptly acute to obtuse, abaxially glabrous (rarely sparsely scabrous), adaxially hirsute, with 5–7 veins and 5–7 adaxial ribs, **sclerenchyma** in fascicles at the margins and abaxially at the veins, rarely small adaxial fascicles, bulliform cells absent. **Inflorescence** paniculate, (2–)3–6 cm long, erect, stiffly open, axis distally scabrous, branches scabrous, a single branch at lower node. **Spikelets** 7–11(–13) mm long, ellipsoid, with (2–)3–4(–5) florets; **glumes** glabrous to scabrous or hispidulous (especially above), subulate to lanceolate or sometimes narrowly ellipsoid, unawned or with an awn up to 0.3 mm long; **lower glumes** (5.8–)6.5–8.5(–9) mm long, lanceolate or ovate, with 1–3 veins; **upper glumes** (6.5–)7–9.5(–10) mm long, with 3–5 veins; **rachilla** up to 1.5 mm long, unilaterally hispidulous opposite to the floret; **lemmas** 6.5–8.5(–9.5) mm long, lanceolate to ellipsoid, scabrous to hirsute, with 5 veins, bidentate or entire, unawned or usually with an awn (0.3–)0.8–2.5(–3.4) mm long; **paleas** 5.5–7.5 mm long, hispidulous between the veins and sometimes on the upper margins, veins with trichomes from the apex to about 2/3(–3/4) to the base; **anthers** (1–)1.2–2 mm long, mostly indehiscent; **ovary** apex glabrous or sparsely hispidulous. **Caryopses** not formed.

Additional collections examined. **MEXICO. México:** Nevado de Toluca, talus slopes and rocky S. rim inside crater, 3 Jul 1964, G. Mick & K. Roe 198. **Tlaxcala:** vertiente NO del volcán La Malinche, zacatonal de *Festuca* y *Calamagrostis*, suelo arenoso, alt. 4080 m, 16 Sep 1986, M. González-Ledesma & P. Vera C. 205; La Malinche volcano, SE of Tlaxcala, NE of Puebla, 19°14'02"N 98°01'56"W, alpine talus and solifluction slopes, plants in close proximity to *F. livida* and *F. hephaestophila*, mostly on windward side of ridges and peak, 4290 m, 22 Sep 1997, S.J. Darbyshire & M. González-Ledesma 4824. **Veracruz:** summit of Cofre de Perote, 19°29'42"N 97°08'55"W, alpine talus and solifluction sites, 4140 m, 20 Sep 1997, S.J. Darbyshire & M. González-Ledesma 4794A.

The inflorescence of the *F. xgonzalez-ledesmae* has the erect appearance of *F. hephaestophila*. The branches may be stiffly spreading, but the lower branch and lower rachis internode are not drooping to pendulous as in *F. livida*. The glumes are broadly to narrowly lanceolate and almost as long as or longer than the adjacent



FIG. 5. *Festuca xgonzalez-ledesmae* holotype, González-Ledesma & Vera 196 (DAO). Scale bar: left = 2 inches; right = 5 cm.

lemmas, whereas they are broadly lanceolate to ellipsoid and distinctly shorter than the adjacent lemmas in *F. hephaestophila*. The lemmas of the hybrid are scabrous to hispid at least in the upper third and sometimes throughout, whereas they are glabrous or only slightly scabrous to hispidulous at the very apex in *F. hephaestophila*. A comparison of additional characters is given in Table 2. In lactophenol cotton blue preparations from the type collection, 0–2% of pollen grains were evenly stained and/or regularly formed. This hybrid was first recognized by Manuel González-Ledesma who described it in some detail (González-Ledesma 1991).

***Festuca xmiscella*** S.J. Darbyshire, nothosp. nov. (*Festuca livida* (Kunth) Willd. ex Spreng.  $\times$  *Festuca tolucensis* Kunth). (**Fig. 6**). TYPE: MEXICO. MÉXICO: E slope of Nevado de Toluca, near gate to crater, 19°15'N 99°45'W, alpine solifluction sites, about 4000 m, 26 Sep 1997, S.J. Darbyshire & M. González-Ledesma 4851 (HOLOTYPE: DAO 811264).

Inter *Festuca livida* et *Festuca tolucensis* intermedia est. Plantae perennes caespitosae, innovationibus intravaginalibus praeditae. Culmi 20–60 cm alti, erecti, scabri ad hispiduli, internodia superne interdum leviter tumida. Vaginae foliorum ima basi tantum integrae, leves vel scabrae, plus minusve inflatae; vaginae foliorum emortuorum in fibras longitudinales non solutae; ligulae (0.5–)1–2.5 mm longae; laminae foliorum conduplicatae, (0.5–)0.7–1.5(–2.1) mm diametri, apice attenuato, abaxialiter glabrae vel scabrae, adaxialiter hirsutae, cum 7–9 nervis, 7–9-costatae, sclerenchymate abaxialiter annulo continuo subepidermali disposito, fasciculis adaxialiter interdum cum venas, cellulis bulliformibus destitutae. Paniculae 5–15(–20) cm longae, laxae et nutantes, axe distali et ramulis scabris. Spiculae 9–14(–16) mm longae, obovatae vel late ellipsoidae, cum 4–6(–7) flosculis; glumae glabrae, scabrae ad hispidulae, subulatae ad lanceolatae, inermiae vel arista usque ad 1 mm longa praeditae; glumae inferiores (6.3–)7–10(–11.5) mm longae, cum 1–3 nervis; glumae superiores (7.5–)8–11(–13.8) mm longae, cum 3–5 nervis; rachillae usque ad 1.5 mm longae, hispidulae unilateraliter; lemmatae (7.5–)8–10(–12) mm longae, lanceolatae, scabrae, papillosae vel hirsutae, cum 5 nervis, apice plerumque bidentata, inermia vel plerumque praedita arista (0–)1–2(–2.9) mm longa; paleae 6–7.5 mm longae, inter venas et in marginalibus distalibus hispidulae, venae prope apicem ad 3/4 cum trichomatibus; antherae 1.5–4.5 mm longae, plerumque indehiscentes; ovarium apex glabrus. Caryopses non praeditae.

Intermediate between *F. livida* and *F. tolucensis*. **Plants** perennial, densely caespitose, shoots intravaginal. **Culms** 20–60 cm tall, erect, scabrous to hispidulous, upper internode sometimes slightly swollen. **Leaf sheaths** closed only at the base, glabrous or scabrous, somewhat loose, not splitting into fibres with age; **ligules** (0.5–)1–2.5 mm long; **leaf blades** conduplicate, (0.5–)0.7–1.5(–2.1) mm in diameter, apex attenuate to a sharp point, abaxially glabrous or scabrous, adaxially hirsute, with 7–9 veins and 7–9 adaxial ribs, **sclerenchyma** in a continuous abaxial band and sometimes with adaxial fascicles at the veins, bulliform cells absent. **Inflorescence** paniculate, 5–15(–20) cm long, lax and nodding, axis glabrous below and scabrous distally, branches scabrous, a single branch at lowest node. **Spikelets** 9–14(–16) mm long, obovate or broadly ellipsoid, with 4–6(–7) florets; **glumes** glabrous, scabrous or hispidulous, subulate to lanceolate, unawned or with an awn up to 1 mm long; **lower glumes** (6.3–)7–10(–11.5) mm long, with 1–3 veins; **upper glumes** (7.5–)8–11(–13.8) mm long, with 3–5 veins; **rachilla** up to 1.5 mm long, unilaterally hispidulous opposite to the floret; **lemmas** (7.5–)8–10(–12) mm long, lanceolate, scabrous, papillose or hirsute, with 5 veins, apex usually bidentate, unawned or usually with a short awn (0–)1–2(–2.9) mm long; **paleas** 6–7.5 mm long, hispidulous between the veins and sometimes on the upper margins, veins with trichomes from the apex to about 3/4 to the base; **anthers** 1.5–4.5 mm long, mostly indehiscent; **ovary** apex glabrous. **Caryopses** not formed.

Additional collections examined. **MEXICO. México:** E slope of Nevado de Toluca, near gate to crater, 19°15'N 99°45'W, alpine solifluction sites, ca. 4000 m, 26 Sep 1997, S.J. Darbyshire & M. González-Ledesma 4849.

The open paniculate inflorescence of the *F. xmiscella* is similar in appearance to that of *F. tolucensis*, but with fewer spikelets (usually less than 20 versus usually more than 20). The lower rachis internode is stiff or somewhat lax, but not pendulous as in *F. livida*. The spikelets are obovate to broadly ellipsoid in *F. xmiscella* with a length to width ratio usually 2 or less. In *F. tolucensis* the spikelets are usually lanceolate or narrowly ellipsoid (occasionally broadly ellipsoid) with a length to width ratio usually 2.5 or greater (occasionally as little as 1.5). The glumes are 3/4 as long as or about as long as the adjacent lemmas, whereas they are usually 1/2 to 3/4 as long as the adjacent lemmas in *F. tolucensis*. A comparison of additional characters is given in Table 2. In lactophenol cotton blue preparations from the type collection, 2–27% of pollen grains were evenly stained and/or regularly formed. This hybrid was first identified and characterized by González-Ledesma (1991).

TABLE 2. A comparison of characteristics of *Festuca hephaestophila*, *F. livida*, *F. toluensis* and their hybrids. Measurements in millimetres.

character	<i>F. hephaestophila</i>	<i>F. ×gonzalez- ledesmae</i>	<i>F. livida</i>	<i>F. ×miscella</i>	<i>F. toluensis</i>
spikelet length	4.5–8.4	7–11(–13)	(9.4)10–17(21)	9–14(–16)	(6.5–)8–14(–18)
lower glume length	2.8–4.5(–5.5)	(5.8–)6.5–8.5(–9)	9.2–15(–20)	(6.3–)7–10(–11.5)	(2.7–)3.5–7.5(–8.6)
upper glume length	3.5–6.3	(6.5–)7–9.5(–10)	9.4–17(–21)	(7.5–)8–11(–13.8)	(3.6–)4.5–8.5(–9.3)
lemma length	4–5.5(–6.2)	6.5–8.5(–9.5)	6.5–12.5	(7.5–)8–10(–12)	(4.6–)5.5–8.5(–10)
anther length	2.2–3.5	(1–)1.2–2	0.8–1.5	1.5–4.5	(2.6–)3–4.5(–5.2)

The following key to species of *Festuca* in Mexico and Central America is largely based on that by Alexeev (1984), but has been updated with additional information and recently described taxa. Although frequently treated in a different genus, *Festuca arundinacea* Schreb. [*Lolium arundinaceum* (Schreb.) Darbysh.; *Schedonorus arundinaceus* (Schreb.) Dumort.] is included in the key and Table 1, because of its similarity to and continued placement in *Festuca* by some authors. The inclusion of *F. ovina* L. is based on Godfrey 66649 report by Pohl (1980) for Costa Rica and accepted by Alexeev (1984). The specimen has not been examined and its identity remains unclear.

KEY TO THE SPECIES OF *FESTUCA* IN MEXICO AND CENTRAL AMERICA

- 1. Leaf blades of shoots usually more than 2 mm wide, flat in cross section, sometimes round in the upper part (or becoming involute or convolute when dry), possessing distinct (wide) bulliform cells.
- 2. Margins of the blade-sheath junction with falcate auricles, more or less provided with cilia \_\_\_\_\_ **F. arundinacea**
- 2. Margins of the blade-sheath junction lacking auricles, without cilia.
- 3. Ligules of culm leaves (1.3–)2–10(–11) mm long.
- 4. Plants loosely caespitose; ligules of culm leaves less than 3.5 mm long; lemmas less than 7 mm long, apex entire, awnless.
- 5. Ligules of culm leaves 2.5–3.5 mm long; leaf blades up to 2 mm wide; lemmas 4–6 mm long; plants of Mexico and Texas \_\_\_\_\_ **F. ligulata**
- 5. Ligules of culm leaves less than 2.5 mm long; leaf blades 1–4 mm wide; lemmas 5.7–6.8 mm long; plants of Costa Rica and Panama \_\_\_\_\_ **F. herrerae**
- 4. Plants densely caespitose; ligules of culm leaves usually 3–8(–11) mm long (sometimes less especially in *F. tancitaroensis*); lemmas greater than 7 mm long, apex bidentate (sometimes entire), with an awn or a mucro (sometimes absent) arising from between the teeth.
- 6. Apex of ovaries densely hispid \_\_\_\_\_ **F. asperella**
- 6. Apex of ovaries glabrous.
- 7. Ligules of culm leaves 1.5–2.8 mm long; lemmas without an awn or at most with a short mucro less than 0.5 mm long \_\_\_\_\_ **F. tancitaroensis**
- 7. Ligules of culm leaves (1.3–)3–8(–11) mm long; lemmas with an awn (0.5–)1–4 mm long.
- 8. Leaf blades stiff, 3–5 mm wide; upper glume (5.5–)6–8.5 mm long \_\_\_\_\_ **F. lugens**
- 8. Leaf blades lax, 1.5–3.6(–6) mm wide; upper glume (3.8–)4–5.6(–6) mm long \_\_\_\_\_ **F. roblensis**
- 3. Ligules of culm leaves not more than 1.5 mm long.
- 9. Lemmas 12–17.5 mm long.
- 10. Lower glumes (1–)2–6(–7.5) mm long; lemmas with 3–5 veins, awns 10–14(–16) mm long \_\_\_\_\_ **F. breviglumis**
- 10. Lower glumes (7.5–)8–9 mm long; lemmas with 5 veins, awns 1.5–3 mm long \_\_\_\_\_ **F. chiriquensis**
- 9. Lemmas 3–9.5(–10) mm long.
- 11. Apex of lemmas bidentate, awns (0.3–)0.5–1.8 mm long arising between the teeth.
- 12. Lemmas 5.5–6.2 mm long, scabrous throughout the back; paleas scabrous along the keels to the base; anthers 2.4–2.7 mm long; apex of ovaries densely hispid; plants of Panama \_\_\_\_\_ **F. swollenii**
- 12. Lemmas 6.5–7 mm long, scabrous on the upper half; paleas scabrous along the keels on the upper third; anthers 3.5–4 mm long; apex of ovaries with a few hairs (1–4); plants of Mexico \_\_\_\_\_ **F. bidenticulata**
- 11. Apex of lemmas without teeth or awns.
- 13. Lemmas 3–4.5 mm long, apex obtuse; anthers 1–1.3 mm long \_\_\_\_\_ **F. subverticillata**



FIG. 6. *Festuca* × *miscella* holotype, Darbyshire & González-Ledesma 4851 (DAO). Scale bar: left = 2 inches; right = 5 cm.

13. Lemmas 5.5–9.5(–10) mm long, apex acute or mucronate; anthers 1.6–4 mm long.
14. Apex of ovaries glabrous.
  15. Leaf blades flat or loosely folded, 1–4 mm wide; spikelets 6.5–9 mm long \_\_\_\_\_ **F. herrerae**
  15. Leaf blades flat, involute or convolute, 3–10 mm wide; spikelets 8–17 mm long.
    16. Dead leaf sheaths more or less breaking up into longitudinal fibres; leaf blades without or with shallow adaxial ribs; panicle branches scabrous or shortly pilose \_\_\_\_\_ **F. amplissima**
    16. Dead leaf sheaths not breaking up into longitudinal fibres; leaf blades with strong adaxial ribs; panicle branches mostly smooth \_\_\_\_\_ **F. jaliscana**
14. Apex of ovaries densely hispid.
  17. Anthers 2.8–4.5(–5) mm long; plants of northeast Mexico \_\_\_\_\_ **F. valdesii**
  17. Anthers up to 2.5 mm long; plants not of Mexico (further south).
    18. Panicle branches smooth or almost smooth; spikelets 6.5–7.5 mm long, with 1–3 florets; anthers 1.7–2 mm long; plants of Guatemala \_\_\_\_\_ **F. aguana**
    18. Panicle branches scabrous; spikelets 8.5–9.5 mm long, with 4–5 florets; anthers 2–2.5 mm long; plants of Panama \_\_\_\_\_ **F. panamica**
1. Leaf blades of shoots usually less than 2 mm in diameter, folded (conduplicate) in cross section, lacking or with indistinct narrow bulliform cells.
  19. Glumes almost as long or longer than the florets (excluding awns) and longer than adjacent lemmas, sometimes with a mucro up to 1.3 mm long; inflorescence nodding, lower rachis internode lax and more or less pendulous \_\_\_\_\_ **F. livida**
  19. Glumes distinctly shorter than the florets and shorter than adjacent lemmas (except in sterile hybrids with *F. livida* keyed below), without a mucro or with a mucro less than 0.3 mm long; panicles erect or nodding, lower rachis internode stiff or lax but not pendulous.
    20. Plants sterile (anthers mostly indehiscent, caryopses not produced); glumes usually more than 3/4 as long as spikelets and about as long as lemmas; plants alpine, growing above tree-line; growing with *F. livida* (Central Mexico).
      21. Plants 4.5–22 cm high, leaf blades with 5–7 veins, sclerenchyma fascicles about as wide as veins; anthers 1–2 mm long \_\_\_\_\_ **F. xgonzalez-ledesmae**
      21. Plants 20–60 cm high, leaf blades with 7–11 veins, sclerenchyma fascicles much wider than veins; anthers 1.5–4.5 mm long \_\_\_\_\_ **F. xmiscella**
    20. Plants usually fertile (anthers usually dehiscent, caryopses produced); glumes usually less than 3/4 as long as spikelets and distinctly shorter than lemmas; plants montane or alpine; growing with *F. livida* or not.
      22. Leaf blades of shoots with one adaxial rib.
        23. Leaf blades of vegetative shoots with 3 veins, sclerenchyma in 7 small abaxial fascicles; apex of ovaries hispid \_\_\_\_\_ **F. bajacaliforniana**
        23. Leaf blades of vegetative shoots with 5–7 veins, sclerenchyma in a continuous or interrupted abaxial band; apex of ovaries glabrous.
          24. Upper glumes usually 2.6–4 mm long; lemmas usually more than 3.3 mm long, with short awns 0.5–2 mm long; anthers (1.4–)2–2.6 mm long \_\_\_\_\_ **F. ovina**
          24. Upper glumes usually 2–3 mm long; lemmas usually less than 3.3 mm long, without awns (rarely mucronate); anthers (1–)1.5–2 mm long \_\_\_\_\_ **F. filiformis**
      22. Leaf blades of shoots with 3–21 adaxial ribs.
        25. Anthers (0.8–)1–1.4(–1.6) mm long.
          26. Spikelets 8–10 mm long; lemmas 6–8.5 mm long, puberulent throughout \_\_\_\_\_ **F. willdenowiana**
          26. Spikelets 6.4–7 mm long; lemmas 5–6 mm long, glabrous or apically scaberulous \_\_\_\_\_ **F. talamancensis**
        25. Anthers greater than 1.5 mm long.
          27. Lemma apex bidentate (sometimes minutely or not at all; examine multiple lemmas), awn (0.3–)0.7–3(–3.7) mm long, arising between the teeth or apex rarely emarginate with the awn arising a little below the apex.
            28. Leaf sheaths usually glabrous; ligules of culm leaves (1–)1.5–3.2(–4.6) mm long; abaxial surface of leaf blades scabrous; sclerenchyma of leaf blades in a continuous or interrupted abaxial band, usually forming pillars and sometimes girders, adaxial fascicles often present \_\_\_\_\_ **F. tolucensis**
            28. Leaf sheaths usually retrorsely scabrous; ligules of culm leaves 0.4–1 mm long; abaxial surface of leaf blades glabrous or slightly scabrous; sclerenchyma of leaf

- blades in a continuous abaxial band, not forming pillars or girders, adaxial fascicles absent \_\_\_\_\_ **F. aequipaleata**
27. Lemma apex entire, without an awn or awned from the apex.
29. Ligules of culm leaves (2–)2.5 mm long or more.
30. Ligules of culm leaves 2.5–3.5 mm long; lemmas 4.5–6 mm long, apex narrowly scarious; anthers 1.5–2.6 mm long \_\_\_\_\_ **F. ligulata**
30. Ligules of culm leaves (2–)5–9.5 mm long; lemmas 5–7 mm long, apex broadly scarious; anthers 2.5–3.3 mm long \_\_\_\_\_ **F. longiligula**
29. Ligules of culm leaves less than or equal 2 mm long.
31. Leaf blades of vegetative shoots (the widest) 1–2 mm in diameter, with 11–23 veins, with 9–21 adaxial ribs.
32. Panicle branches smooth; paleas scabrous along the keels on the upper  $\frac{2}{3}$  –  $\frac{3}{4}$ ; apex of ovaries glabrous; plants of Costa Rica and Panama \_\_\_\_\_ **F. cartagana**
32. Panicle branches scabrous; paleas scabrous along the keels on the upper  $\frac{1}{3}$  –  $\frac{1}{2}$ ; apex of ovaries hispid; plants of Mexico \_\_\_\_\_ **F. orizabensis**
31. Leaf blades of vegetative shoots always 0.3–1(–1.2) mm in diameter (sometimes wider in *F. rubra*), with 5–9 veins, with 3–7 adaxial ribs.
33. Leaf blades of vegetative shoots with abaxial sclerenchyma in a continuous band, rarely interrupted.
34. Leaf blades of vegetative shoots up to 0.5 mm in diameter, with 5(–7) veins, adaxial surfaces with hairs 50–80  $\mu$ m long; junction of blades and sheaths swollen (callose auricles) \_\_\_\_\_ **F. callosa**
34. Leaf blades of vegetative shoots 0.6–0.8 mm in diameter, with 7–9 veins, adaxial surfaces with hairs 20–30  $\mu$ m long; junction of blades and sheaths not swollen (auricles not callose).
35. Margins of leaf sheaths of vegetative shoots closed up to  $\frac{2}{3}$ ; ligules of culm leaves 0.2–0.6 mm long; leaf blades usually glauco-pruinose; lemmas 6.5–7 mm long, not awned; apex of ovaries densely hispid \_\_\_\_\_ **F. hintoniana**
35. Margins of leaf sheaths of vegetative shoots closed up to  $\frac{1}{3}$ ; ligules of culm leaves 0.5–1 mm long; leaf blades green, not glaucous or pruinose; lemmas 5–5.2 mm long, awns 2–2.2 mm long; apex of ovaries glabrous \_\_\_\_\_ **F. beamanii**
33. Leaf blades of vegetative shoots with abaxial sclerenchyma in fascicles.
36. Leaf blades of vegetative shoots always with 5 veins, with 3 adaxial ribs.
37. Margins of leaf sheaths of vegetative shoots closed from the base to near the top; dead leaf sheaths not breaking up into longitudinal fibres; leaf blades abaxially more or less scabrous or rarely glabrate, adaxially with dense trichomes, small adaxial fascicles of sclerenchyma usually present; paleas scabrous along the keels on the upper  $\frac{1}{3}$ ; apex of ovaries with a few hairs, rarely glabrous; plants alpine \_\_\_\_\_ **F. hephaestophila**
37. Margins of leaf sheaths of vegetative shoots closed from the base to  $\frac{1}{3}$ ; dead leaf sheaths more or less breaking up into longitudinal fibres; leaf blades abaxially smooth (glabrous), adaxially smooth or almost so, adaxial fascicles of sclerenchyma absent; paleas glabrous along the keels; apex of ovaries glabrous; plants montane \_\_\_\_\_ **F. rzedowskiana**
36. Widest leaf blades of vegetative shoots with 7–9 veins, with 3–7 adaxial ribs.
38. Plants laxly caespitose, often with short rhizomes; margins of leaf sheaths of vegetative shoots closed from the base to at least  $\frac{1}{2}$ ; lemmas with an awn greater than 1 mm long \_\_\_\_\_ **F. rubra**
38. Plants more or less densely caespitose, without rhizomes; margins of leaf sheaths of vegetative shoots closed from the base

to not more than 1/3; lemmas awnless or sometimes with an apical mucro up to 1 mm long.

39. Anthers in lower floret in the spikelets usually abortive, those of upper florets well-developed and 3–4.2 mm long \_\_\_\_\_ **F. diclina**

39. Anthers in lower florets of the spikelet not abortive, all anthers more or less the same length, 1.6–6 mm long.

40. Some or all shoots extravaginal (although plants caespitose); adaxial surface of leaf blades of vegetative shoots with a few isolated trichomes 20–40 µm long; anthers 1.6–2.3 mm long.

41. Ligules 0.1–0.2 mm long; spikelets 10.5–11.5 mm long, with 5–6 florets; lemmas 6.5–7.5 mm long

\_\_\_\_\_ **F. guatemalica**

41. Ligules 0.3–2 mm long; spikelets 6.5–9 mm long, with 3–5 florets; lemmas 5.7–6.8 mm long

\_\_\_\_\_ **F. herrerae**

40. All shoots intravaginal; adaxial surface of leaf blades of vegetative shoots with dense trichomes 50–100 µm long; anthers greater than 2.5 mm long.

42. Blades of leaves always folded (conduplicate or convolute), 0.3–0.6 mm in diameter, with 5–7(–9) veins; panicles more or less dense, branches erect; apex of ovaries glabrous (rarely with a few hairs)

\_\_\_\_\_ **F. rosei**

42. Blades of culm leaves flat to loosely folded (conduplicate), (0.4–)0.6–1.2 mm in diameter, with 9–11 veins; panicles open, branches lax; apex of ovaries more or less hispid (rarely glabrous)

\_\_\_\_\_ **F. pringlei**

#### ACKNOWLEDGMENTS

I am grateful to Jacques Cayouette, Manuel González-Ledesma, Jochen Müller and Barbara Wilson for their useful comments and discussions, to Jacques Cayouette and Jochen Müller for assistance with the Latin descriptions, and to herbarium curators at ARIZ, DAO, TEX, US and WIS for making specimens available for study. Manuel González-Ledesma was of invaluable assistance with field work.

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